

COELOPHYSIDS (DINOSAURIA:THEROPODA) FROM THE UPPER TRIASSIC (REVUELTIAN) SNYDER QUARRY

ANDREW B. HECKERT, KATE E. ZEIGLER, SPENCER G. LUCAS and LARRY F. RINEHART

New Mexico Museum of Natural History and Science, 1801 Mountain Road NW, Albuquerque, NM 87104-1375

Abstract—The Snyder quarry preserves one of the richest assemblages of Norian theropods in the world, and the second-most productive theropod locality in the Chinle Group. At least four coelophysid theropods are preserved at the Snyder quarry, based on tibiae. Most elements of these theropods are represented, including an incomplete skull and lower jaws, cervical, dorsal, sacral, and caudal vertebrae, a scapulocoracoid, ilia, ischia, femora, tibiae, a fibula, astragalocalcanea, and diverse carpals and tarsals. These specimens demonstrate that the Snyder quarry theropods pertain to the Revueltian theropod *Eucoelophysis*, only known from the type locality at Orphan Mesa 10 km to the east and Baldwin's original collection described by Cope in 1881. Theropod dinosaurs at the Snyder quarry are the most abundant terrestrial predators, and outnumber rauisuchians and spheosuchians. These theropods are, with the "Padian theropod" from the same unit in the Petrified Forest National Park and *Procompsognathus* from the Stubensandstein in Germany, part of an apparently Pangean radiation of coelophysid theropods during Revueltian (early-mid Norian) time.

Keywords: Norian, theropod, ceratosaur, *Eucoelophysis*

INTRODUCTION

The Snyder quarry (NMMNH locality 3845) in north-central New Mexico is an extraordinarily rich bonebed that preserves an archosaur-dominated vertebrate assemblage that appears to represent the aftermath of a catastrophic event (Heckert et al., 2000a; Zeigler, 2003). Ever since its first discovery, one of the most significant aspects of the Snyder quarry is the relatively frequent occurrence of theropod dinosaurs (Heckert and Zeigler, 2003). Heckert et al. (2000a) published a preliminary description of these theropods, which are all derived (coelophysid-grade) ceratosaurs that appear to represent two taxa—a smaller, more gracile form (most of the fossils) and a second, larger taxon thus far represented by a single fused tibia-fibula-astragalocalcaneum. Presently we are preparing another manuscript describing an incomplete skull and lower jaws of the smaller taxon, but use this paper as an opportunity to update the descriptions and interpretations of Heckert et al. (2000a).

STRATIGRAPHY AND AGE

The Snyder quarry is in the Painted Desert Member of the Petrified Forest Formation, 28.5 m below the contact with the overlying Rock Point Formation (Fig. 1). This stratigraphic position is approximately equivalent to the Canjilon quarry 4 km to the east. The Snyder quarry also appears to be at nearly the same stratigraphic horizon as the type locality of *Eucoelophysis baldwini* Sullivan and Lucas near Orphan Mesa (Sullivan et al., 1996; Sullivan and Lucas, 1999; Lucas et al., 2002, 2003). All of these localities are much lower stratigraphically than the famous Whitaker (*Coelophysis*) quarry at Ghost Ranch, which is at least 50 m above the aforementioned theropod localities and in an entirely different unit, the Rock Point Formation.

The presence of the phytosaur *Pseudopalatus* and the aetosaur *Typhorax coccinarum* Cope indicates a Revueltian (early-mid Norian) age for the Snyder quarry (Heckert et al., 2000a). This age assignment also confirms that the Snyder quarry theropods are older than the *Coelophysis* quarry at Ghost Ranch, as the latter includes the phytosaur *Redondasaurus*, and thus is of Apachean (late Norian-Rhaetian) age (Lucas, 1998; Lucas et al., 2003).

The Petrified Forest Formation in north-central New Mexico is stratigraphically equivalent to the Painted Desert Member of the Petrified Forest Formation in west-central New Mexico and Arizona and the Bull Canyon Formation in east-central New Mexico and West Texas

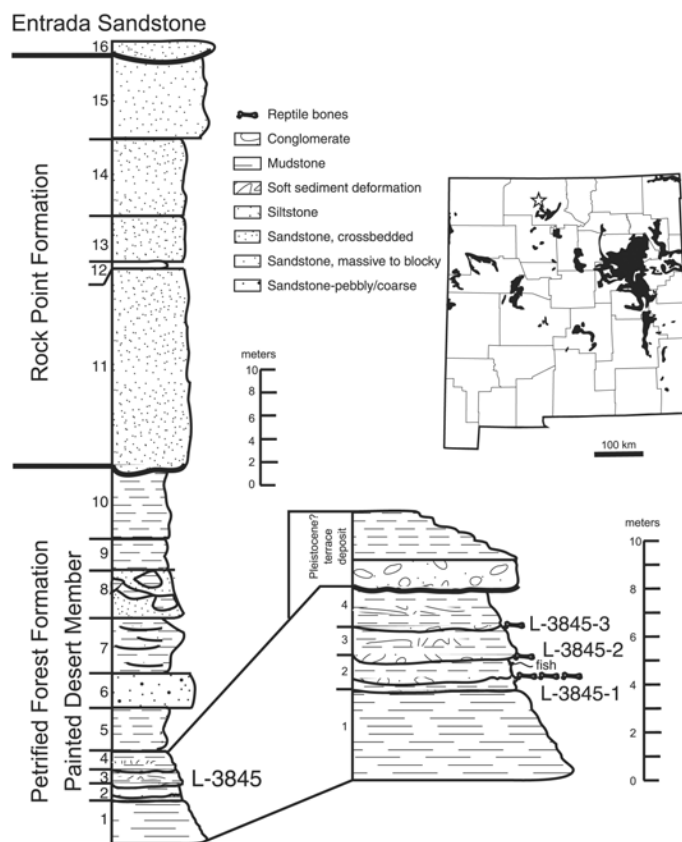


FIGURE 1. Index map showing location of the Snyder quarry site in north-central New Mexico, distribution of Triassic outcrops (from Heckert et al., 2000), and a stratigraphic section at the quarry.

(Lucas, 1993, 1997; Lucas et al., 2002, 2003). Thus, the Snyder quarry is broadly correlative to the upper faunas of the Petrified Forest National Park (e.g., Murry and Long, 1989; Hunt and Lucas, 1995), Bull Canyon Formation faunas in eastern New Mexico (Hunt, 1994, 2001) and the Post quarry in Texas (Small, 1989; Long and Murry, 1995).

TAPHONOMY

The Snyder quarry consists of three primary fossiliferous horizons in a series of fining-upwards sequences in a prominent grayish-green band of sediment (Fig. 1). Each of these sequences generally consists of a basal pebble conglomerate that fines up through a very thin (<5 cm) muddy sandstone/sandy mudstone (wacke) into a 1-1.5-m-thick laminated mudstone-dominated bed. The vast majority of the fossil bones, including all of the dinosaur material described here, are found in the basal sequence, in either the mudstone-pebble conglomerate or the immediately overlying sandstone-wacke interval (base of unit 2 in Figure 1). This interval is sometimes referred to in NMMNH records as locality 3845-1. Fossils from the other two fining-upwards cycles are designated as locality 3845-2 and locality 3845-3, respectively. Some theropod fossils, principally vertebrae and possible metapodials, occur in these higher conglomeratic layers, but this material is isolated and, quite possibly, reworked from the lower levels.

Generally, most of the bones from the lower level (3845-1) are loosely associated, but they are not articulated. However, at least half of the theropod specimens are much more closely associated, with some elements articulated. Thus, while many of the theropod specimens we discuss below are given different specimen numbers in the NMMNH catalog, they probably only pertain to a few individuals, possibly as few as four. Zeigler (2002, 2003) documented the likely catastrophic origin of the Snyder quarry, apparently in the aftermath of a large forest fire. Perhaps because of their lighter bodies, the theropod fossils all appear to be at or near the top of the lowest bone-bearing interval. Because of the extremely fragile nature of these fossils, including bones <1 mm thick, it is obvious that these fossils were not transported far. Furthermore, the skull and jaws preserve many teeth, indicating that the animals were not in an advanced state of decomposition, as opposed to the phytosaur skulls from the quarry, most of which have few teeth preserved *in situ* (e.g., Zeigler et al., 2002, 2003).

To date, the theropod fossils have all come from a narrow spatial interval as well, generally corresponding to the southwestern limit of the original quarry wall. These fossils were generally found early in the excavations, and jacket 3 (large coelophysid), 4 (head of small ischium and associated elements), 5 (small sacrum), 11 (skull) and 18(?) (other postcrania) were all excavated in 1998 or early in the 1999 field season. These elements and the two relatively complete femora (excavated with an associated tibia and fibula without jacketing in 1998) all came from the south-central portion of the original face. Although most of these fossils were collected prior to establishing a grid (in 1999), all but the large coelophysid were recovered from an area smaller than 2x2 m. The third small individual was found farther to the north and west, with the tibia collected from jacket 34 and a small ilium eventually prepared from jacket 24, which had been removed from just to the north and west of where jacket 34 came out. When these data are combined with the nearly uniform size of the elements and articulation of some, we believe that there is a strong possibility that most of the small theropod material preserved at the main bone bed pertains to just these three individuals.

DESCRIPTION

Theropod fossils at the Snyder quarry are, by Chinle standards, abundant and exceptionally well preserved. Two taxa, one considerably larger than the other, are represented. The majority of the theropod fossils pertain to the smaller morphotype and include an incomplete skull, lower jaws, and two articulated cervical vertebrae (Figs. 2A, 3A-B), a dorsal vertebra, an incomplete sacrum, an incomplete left scapulocoracoid (Fig. 3C), fragmentary right ilium (Figs. 2C, 3E), nearly complete right ischium (Fig. 2B, 3D), two femora (Figs. 2D, 3F), three tibiae (Figs. 2E-F, 3G), an astragalus, and numerous vertebrae, metapodials, phalanges, and ribs. The larger taxon is represented solely by an incomplete, fused tibia, fibula, astragalus, and calcaneum (Figs.

2G, 3H). All of the limb bones are hollow, and are preserved with thick calcite infilling surrounded by the comparably thin bone walls of the limb shafts. The vertebrae are similarly hollow. We briefly and preliminarily describe these theropod fossils and discuss their affinities here.

Skull

The preserved skull (NMMNH P-30852) material includes a nearly complete left premaxilla and maxilla and a left lacrimal as well as several more fragmentary posterior elements (Fig. 2A). Of these, the premaxilla and lacrimal have now been prepared out separately. The premaxilla was slightly disarticulated and rotated so that it is viewed occlusally in Figure 2A. Were it rotated back into position, there would be a distinct subnarial gap, the distinctive trait of most ceratosaurs (Rowe and Gauthier, 1990). It has now been prepared out and is completely free of matrix. The anterior margin of the antorbital fenestra is bounded by the dorso-posteriorly projecting ascending process of the maxilla, as is typical of coelophysids. The lacrimal has been prepared out since we tentatively identified it (Heckert et al., 2000a) (Fig. 3B).

Lower jaw

Both the right and left dentaries are preserved, together with incomplete angulars and surangulars, a left splenial and a possible ceratobranchial. The dentaries are slender and elongate. The surangular is moderately deep and appears somewhat more robust than that of *Coelophysis* or *Megapnosaurus* (= *Syntarsus*) (see Ivie et al., 2001 regarding the use of the name *Megapnosaurus* in place of *Syntarsus*).

Teeth

There are four very small teeth or alveoli visible in the premaxilla. These teeth, anterior to the subnarial gap, follow the pattern observed in *Megapnosaurus* (Raath, 1977, 1990) and *Coelophysis* (Colbert, 1989, 1990), where premaxillary teeth are much smaller than maxillary teeth or most dentary teeth. The maxilla contains at least 24 sockets, 9 of which contain teeth in varying stages of eruption. The right dentary possesses 24 identifiable sockets, four of which contain nearly complete, fully erupted teeth, and six more contain incomplete teeth. The left dentary preserves 15 teeth and 9 additional sockets, two of which have the tips of replacement teeth emerging. These yield tooth counts were similar to the 25-27 teeth per row documented by Paul (1993). The teeth are all laterally compressed and strongly recurved. The maxillary and dentary teeth are approximately subequal in size, but both are considerably larger than the tiny premaxillary teeth. This is the oldest occurrence of marked heterodonty in theropods.

Vertebral column

Two cervical vertebrae were found articulated with the skull (Fig. 2A). These may correspond to the third or fourth (or, possibly, fourth and fifth) cervicals. They are low, elongate, and deeply pleurocoelous with greatly reduced neural spines. These and another cervical vertebra all possess elongate, extraordinarily delicate, cervical ribs. The rod-like ribs all extend posteriorly such that they cover at least one more vertebra in the series, and probably extended even further posteriorly, but are not preserved completely.

The best-preserved dorsal vertebra is amphicoelous, taller, and more robust than the cervicals. The sacrum (part of a single specimen designated NMMNH P-31661) consists of five fused vertebrae. The first four of these are thoroughly fused across both their articular surfaces and their neural processes. The last sacral is a sacro-caudal and is less strongly fused across its articular facets, but still well-fused across the neural arches.

Scapulocoracoid

The incomplete left scapulocoracoid (part of NMMNH P-31661) lacks approximately half of the scapular blade but is otherwise nearly

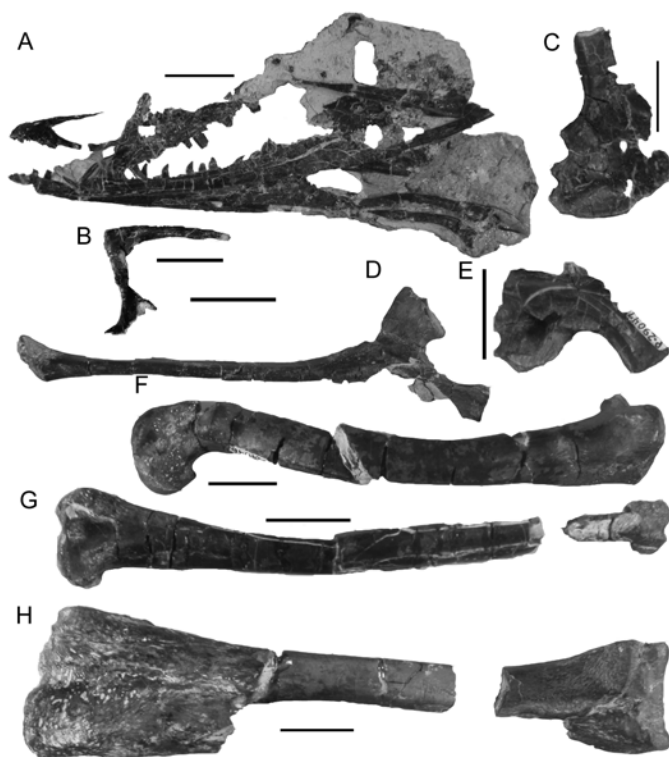


FIGURE 2. Coelophysoid theropods from the Snyder quarry. **A**, NMMNH P-30852, incomplete skull, lower jaws, and articulated cervical vertebrae in left lateral view; **B**, NMMNH P-39047, incomplete right ischium in lateral view; **C**, incomplete right ilium of the same specimen in lateral view; **D** NMMNH P-29046, right femur in posterior view; **E-F**, NMMNH P-31293, nearly complete, slightly crushed left tibia in **E**, anterior and **F**, posterior views; **G**, NMMNH P-29168, large coelophysoid, incomplete fused tibia-fibula-astragalus-calcaneum. All are approximately 40% actual size. Abbreviations: **a** = acetabulum; **af** = acetabular facet; **as** = astragalus; **ats** = appressed tibial surface; **bf** = brevis fossa; **ca** = calcaneum; **cb?** = ceratobranchial?; **cr** = cervical rib; **cv** = cervical vertebra; **f** = fibula; **gt** = greater trochanter; **if** = iliac facet; **l** left lacrimal; **mx** = maxilla; **pmx** = premaxilla; **sa** = surangular; **sac** = supra-acetabular crest; **t** = tooth; **ti** = tibia.

complete. In lateral view, the scapula is more symmetrical at the level of the glenoid (anterior projection = posterior projection of the acromion) than illustrated for *Coelophysis* (Colbert, 1989) or *Megapnosaurus* (Raath, 1977; Tykoski, 1998). This element is somewhat similar to *Eucoelophysis* (Sullivan and Lucas, 1999), but the glenoid is more arcuate and the scapula as a whole more gracile than that taxon, although this may be an artifact of the larger size of the holotype of *Eucoelophysis*. The coracoid possesses a strong glenoid pillar and is likewise more expanded than illustrated in the other coelophysoids.

Ilium

Only two fragmentary ilia are known. The more fragmentary specimen (NMMNH P-29047; Fig. 2C) was found articulated with the right ischium (Fig. 2B) and demonstrates the presence of a very large, entirely open acetabulum. A prominent supra-acetabular crest curves laterally over the acetabulum and the anterior margin of the brevis fossa. Both the ischial and pubic pedicles are preserved and are roughly subequal in length. The second ilium was more complete, but was not articulated with any other elements. It is very similar to the illustrated ilia of *Coelophysis* and *Syntarsus*, and is relatively low and elongate,

with a deep brevis shelf protruding over the open acetabulum.

Ischium

The ischium (NMMNH P-29047) is straight and elongate, with only a modest distal swelling for the ischial boot (Figs. 2B,3D). The dorsally projecting iliac and acetabular facets are well-developed, as is the anteriorly projecting pubic process.

Femur

Right and left femora (both assigned to NMMNH P-29046) were found in close association with other hind limb elements in 1998. The femora are marked by a medially offset head that is slightly “hooked” in anterior or posterior view (Fig. 2D). This is more strongly developed than in *Eucoelophysis* or illustrated by Colbert (1989) for *Coelophysis*, yet less strong than that seen in *Megapnosaurus rhodesiensis*. The femora lack the proximal groove or sulcus of *Eucoelophysis*. The anterior or lesser trochanter is a prominent subtriangular ridge. Although this differs from the condition in *Eucoelophysis*, it corresponds to the “robust” morph of *Megapnosaurus* (Raath, 1977, 1990; Tykoski, 1998), whereas *Eucoelophysis* corresponds to the gracile morph (Sullivan and Lucas, 1999).

Tibia

There are portions of three small coelophysoid left tibiae from the Snyder quarry. One is essentially complete, a second nearly so (NMMNH P-31293—Fig. 2E-F) and a third consists solely of the proximal end and was found beneath the ilium and ischium. The most striking feature of the tibia is the strongly appressed surface that was held in contact with the fibula. This condition exactly matches that of *Eucoelophysis* and differs from *Megapnosaurus* and *Coelophysis*, although the articulated nature of specimens of the latter makes this condition difficult to assess in the Ghost Ranch theropod sample (Downs, 2000). There is no evidence of fusion of the tibiae to more distal elements on either specimen for which a distal tibia is preserved. There is, however, a marked hollow in the base of the tibia to accept the ascending process of the astragalus.

Fibula

Two incomplete fibulae are known. Relative to the tibiae they are greatly reduced and, as described above, fit against an appressed surface on the tibia. There is no evidence of fusion of the fibula to the tibia or to distal elements.

Astragalocalcaneum

There are two astragali preserved and in the collections, but only one is sufficiently well preserved to describe. This left element (NMMNH P-35379) has the calcaneum solidly fused to it such that the suture is almost invisible. The ascending process is low and somewhat triangular in anterior view, with a slightly beveled proximal surface. The calcaneum is greatly reduced and essentially only a semicircular disk in lateral view, with a minimal contribution to the element as a whole. The fibular facet is the deepest excavation on the proximal face, followed by the tibial facet and the intervening groove.

Other elements

To date, we have recovered numerous metapodials and phalanges, as well as a large number of posterior cervical, dorsal, and caudal vertebrae. Pending further cleaning and preparation these will be detailed in a later work, but we note here that the phalanges and metapodials are gracile, with greatly reduced shafts relative to their articular ends. Unprepared material includes additional femora and tibiae as well as other axial skeletal elements.

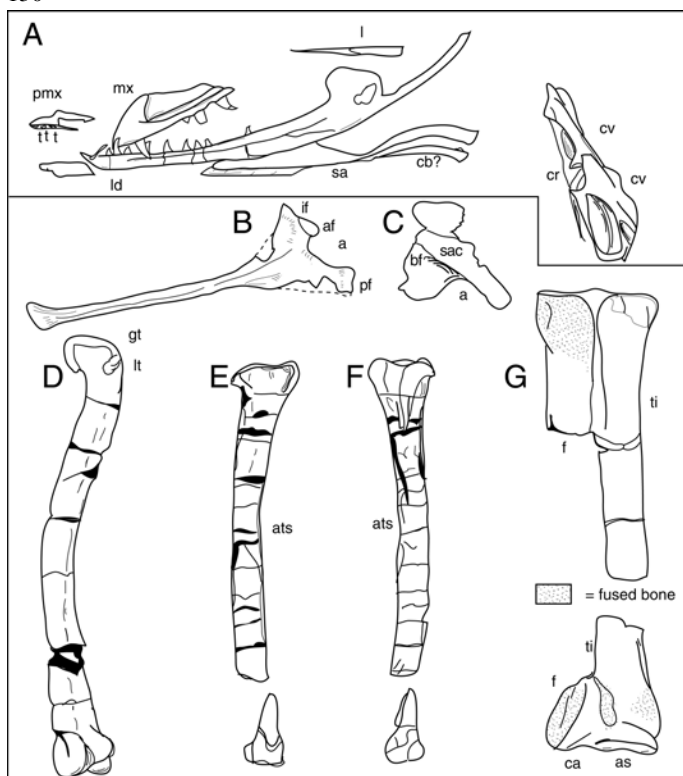


FIGURE 3. Photographs of selected coelophysid elements from the Snyder quarry. **A**, NMMNH P-30852, incomplete skull and lower jaws in lateral view; **B**, left lacrimal from the same specimen in medial view; **C**, NMMNH P-31661, incomplete left scapulocoracoid in medial (internal) view; **D**, NMMNH P-29047, right ischium in lateral view; **E**, incomplete right ilium of the same specimen in lateral view; **F**, NMMNH P-29046, left femur in anterior view; **G**, NMMNH P31293, incomplete left tibia in posterior view; **H**, NMMNH P-29168, large coelophysoid, incomplete fused tibia-fibula-astragalus-calcaneum. All scale bars = 2 cm.

Larger coelophysoid

Preparation of the third jacket removed from the quarry yielded a large, nearly complete tibia-fibula-astragalus-calcaneum (NMMNH P-29168). The most striking aspect of this bone is the fusion not only of the distal tibia and fibula to the astragalus and calcaneum, but the complete fusion of the proximal fibula to the tibia (Fig. 2G). Although this extensive fusion has resulted in large areas of slightly rugose bone surfaces, this texture is still relatively smooth and not obviously pathological, and could represent an “aberrant segmentation failure” rather than a pathology (D. Tanke and B. Rothschild, pers. comm.). Furthermore, the shafts of the tibia and fibula are neither fused nor appressed. The former condition precludes assignment to *Eucoelophysis*, and the latter provides additional argument against a pathological origin for the fused bone. The tibia and fibula are hollow and filled with calcite. The prominent ascending process of the astragalus is still distinct beneath the fused bone surface, also supporting a theropod identification for these bones, and the fusion, if not pathological, is a feature typical of derived ceratosaurs.

Affinities

The subnarial gap, heterodont premaxilla, gracile limb bones, and numerous other features all support assignment of the smaller theropod to the Ceratosauria and, more specifically, to the Coelophysoidea (Rowe and Gauthier, 1990; Holtz, 1994, 2000). However, the coelophysoid taxa *Eucoelophysis*, *Coelophysis*, and *Megapnosaurus* are exceedingly similar in many details of the skeleton, so much so that some authors have stated, either explicitly (Paul, 1993) or implicitly (Downs, 2000), that all of these taxa should be

assigned to a single genus. Thus, while we have documented numerous differences between the Snyder quarry theropods and other coelophysoid taxa, we take the conservative approach here and choose not to erect a new name. In general, the smaller coelophysoid most closely resembles *Eucoelophysis*, particularly in details of the scapulocoracoid, ischium, and tibia. Some of the differences between these theropods and *Eucoelophysis* may warrant erection of a new species, but many of these differences, particularly in the femur, could be sex-related, as posited by Raath (1977). Thus, we tentatively refer the smaller theropod to *Eucoelophysis* sp. The larger theropod is too fragmentary to identify with certainty, but this specimen certainly appears unique among ceratosaurs.

SIGNIFICANCE

The theropods from the Snyder quarry are important for several reasons: (1) dinosaurs are a relatively rare component of almost all Chinle faunas; (2) these theropods are some of the best-preserved early coelophysoids; (3) their stratigraphic position, roughly correlative to the type locality of *Eucoelophysis baldwini*, enhances our understanding of the superposition of Upper Triassic dinosaur faunas; and (4) all of these combine to improve our understanding of Late Triassic dinosaur evolution.

As mentioned previously, dinosaurs in general are a rare component of Chinle faunas. Although the theropods described here are numerically and volumetrically a relatively small component of the Snyder quarry fauna, the presence of four individual theropods of two taxa qualifies this as the second-most productive Chinle theropod site. Aside from the *Coelophysis* Lagerstätte, no other Chinle locality preserves either this diversity or number of theropod body fossils. To date, theropod fossils greatly outnumber those of other terrestrial archosaurian predators at the quarry, and even MNI counts of the theropods (4) outnumber the combined MNI of rauisuchians (2) and sphenosuchians (1) (Zeigler et al., 2003).

The Snyder quarry vertebrate fossils are, in general, exquisitely preserved. This is especially true of the coelophysoid theropods. Indeed, the coelophysoids present a taphonomic problem—how to preserve delicate elements such as the skull, cervical ribs, and pelves of the coelophysoids in the same depositional regime that was transporting phytosaur skulls and postcrania? We accept Zeigler’s (2002, 2003) hypothesis of a catastrophic origin of the Snyder quarry, and note that this catastrophic event the coelophysoid fossils from the Snyder quarry are the best preserved of any Chinle theropod fossils outside of the *Coelophysis* quarry.

Indeed, the Snyder quarry theropods are the best-preserved pre-Apachean coelophysoid theropods in the world. Presently, the worldwide body fossil record of Revueltian theropods consists primarily of a handful of taxa, based on a few fragmentary records from North America, and *Procompsognathus* and *Halticosaurus* from the Stubensandstein in Germany (Heckert and Lucas, 2000; Heckert, 2001). Prior to the discovery of the Snyder quarry theropods, the most complete Revueltian theropods from the Chinle Group were the large ceratosaur *Gojirasaurus* (Carpenter, 1997), the coelophysid *Eucoelophysis baldwini* (Sullivan and Lucas, 1999) and the so-called “Padian theropod,” a coelophysid from the Painted Desert Member of the Petrified Forest National Park first described by Padian (1986). These theropods collectively indicated that a transition in the theropod guild from herrerasaurid-dominated faunas typical of Otischalkian and Adamanian (Carnian-aged) strata to ceratosaur-dominated faunas in the Norian and into the Early Jurassic (Hunt et al., 1998; Heckert and Lucas, 2000; Heckert et al., 2000b; Heckert, 2001). Both *Eucoelophysis* and the “Padian theropod” have traditionally been considered coelophysids, as has, occasionally, *Procompsognathus* (Ostrom, 1981; but see Norman, 1990; Sereno and Wild, 1992). The problematic taxon *Protoavis* probably represents, at least in part, a coelophysid theropod. In particular, the reconstructed femora illustrated by Chatterjee (1999, fig. 19), although composites

of individuals from two different formations(!), closely resemble those of the Snyder quarry theropod and other coelophysids. The type locality of *Protoavis*, the Post quarry in West Texas, is in the Bull Canyon Formation and also of Revueltian age (Lucas et al., 1994).

However, none of these taxa, included well-preserved, unambiguously associated skull material (Serenio and Wild, 1992; Carpenter, 1997; Chatterjee, 1999; Sullivan and Lucas, 1999; Heckert and Lucas, 2000). One fact that is apparent from the Snyder quarry theropod material is that, beyond the synapomorphies associated with Coelophysidae (e.g., Holtz, 1994, 2000), is that the coelophysid *bauplan* was established by Revueltian time. Specifically, the anatomy of the Snyder quarry theropods is extremely similar to that of *Coelophysis* (Colbert, 1989, 1990) and *Megapnosaurus* (= *Syntarsus*) (Raath, 1977, 1990). The skull is elongate and spectacularly gracile. The entire skeleton, in fact, is gracile and highly specialized. The cervical vertebrae have well-developed pleurocoels and extremely thin, elongate ribs that extend posteriorly over at least one more centrum. The girdles are thin, and the sacrum includes five coossified vertebrae. The preserved limbs are also gracile, and the femora and tibiae are all but identical to some specimens of *Coelophysis* and *Megapnosaurus*. The astragalus is fused to the calcaneum, but curiously, not to the tibia and fibula.

The Chama basin in northern New Mexico is the first location in the Chinle Group with two clearly superposed theropod faunas. The lower fauna includes the type of *Eucoelophysis baldwini* and the Snyder quarry theropods, which we have amply demonstrated to be of Revueltian age. Overlying these theropods, in the Rock Point Formation, is the *Coelophysis* Lagerstätte, of younger, Apachean (latest Norian-Rhaetian?) age (Lucas et al., 2003, and references cited therein). Thus, material at the Snyder quarry, the type of *Eucoelophysis*, and at least some of Baldwin's original material named *Coelophysis* by Cope are demonstrably older than the *Coelophysis* material discovered by G.H. Whitaker for E.H. Colbert at Ghost Ranch.

The stratigraphic range of coelophysoids is now well established and reasonably well constrained, facilitating a better understanding of the early evolution of the dinosaurs (Heckert and Lucas, 2000b). During the Adamanian, very early in the evolution of dinosaurs, the fused tibia-fibula-astragalus-calcaneum that is the hallmark of derived ceratosaurs appears in *Camposaurus arizonensis* Hunt et al. (Lucas et al., 1992; Long and Murry, 1995; Hunt et al., 1998). By Revueltian time, ceratosaurs are marginally more abundant and, as the fossils described here demonstrate, have evolved into a body form classically identified as coelophysoid. Indeed, this design would prove so successful that it would remain essentially the same through the later evolution of *Coelophysis* and both species of *Megapnosaurus*: *M. kayentakatae* and *M. rhodesiensis*, the latter of which would not become extinct until nearly 185 Ma. With the possible exception of some of the more plesiomorphic titanosaurid sauropods, no other group of dinosaurs has retained such a consistent body form for such a considerable (approximately 30 Myr) span of time.

ACKNOWLEDGMENTS

This work would have been impossible without the determination and effort of volunteers too numerous to list here. We are especially indebted to the New Mexico Friends of Paleontology and other NMMNH volunteers for the time and effort necessary to excavate, collect, prepare, and catalog the tetrapod fauna of the Snyder quarry. Funding from the Society of Vertebrate Paleontology (Bryan Patterson award to ABH), New Mexico Geological Society (Grants-in-aid to KEZ), and the New Mexico Friends of Paleontology supported work at the Snyder quarry. The New Mexico Museum of Natural History provided logistical support. Kim Murphy of the University of New Mexico real estate office permitted work at the Snyder quarry. Hillary Jenkins photographed the specimens in Figure 3.

REFERENCES

- Carpenter, K., 1997, A giant coelophysoid (Ceratosauria) theropod from the Upper Triassic of New Mexico, U.S.A.: Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, v. 205, p. 189-206.
- Chatterjee, S., 1999, *Protoavis* and the early evolution of birds: Palaeontographica Abteilung A, v. 254, p. 1-100.
- Colbert, E. H., 1989, The Triassic dinosaur *Coelophysis*: Museum of Northern Arizona Bulletin, v. 57, p. 160.
- Colbert, E. H., 1990, Variation in *Coelophysis*, in Carpenter, K., and Currie, P. J., eds., Dinosaur systematics: Approaches and perspectives: Cambridge, Cambridge University Press, p. 80-90.
- Cope, E. D., 1887, The dinosaurian genus *Coelurus*: American Naturalist, v. 21, p. 367-369.
- Downs, A., 2000, *Coelophysis bauri* and *Syntarsus rhodesiensis* compared, with comments on the preparation and preservation of fossils from the Ghost Ranch *Coelophysis* quarry: New Mexico Museum of Natural History and Science Bulletin, v. 17, p. 33-37.
- Heckert, A. B., 2001, The microvertebrate record of the Upper Triassic (Carnian) lower Chinle Group, southwestern U.S.A. and the early evolution of dinosaurs [Ph.D. dissertation]: Albuquerque, University of New Mexico, 465 p.
- Heckert, A. B., and Lucas, S. G., 1999, Global correlation and chronology of Triassic theropods (Archosauria: Dinosauria): Albertiana, v. 23, p. 22-35.
- Heckert, A. B., and Lucas, S. G., 2000, Global correlation of the Triassic theropod record: Gaia, v. 15, p. 63-74.
- Heckert, A. B., Zeigler, K. E., Lucas, S. G., Rinehart, L. F., and Harris, J. D., 2000a, Preliminary description of coelophysoids (Dinosauria: Theropoda) from the Upper Triassic (Revueltian: early-mid Norian) Snyder quarry, north-central New Mexico: New Mexico Museum of Natural History Bulletin, v. 17, p. 27-32.
- Heckert, A. B., Lucas, S. G., and Sullivan, R. M., 2000b, Triassic dinosaurs in New Mexico: New Mexico Museum of Natural History and Science Bulletin, v. 17, p. 17-26.
- Holtz, T. R., Jr., 1994, The phylogenetic position of the Tyrannosauridae: implications for theropod systematics: Journal of Paleontology, v. 68, p. 1110-1117.
- Holtz, T. R., Jr., 2000, A new phylogeny of the carnivorous dinosaurs: Gaia, v. 15, p. 5-61.
- Hunt, A. P., 1994, Vertebrate paleontology and biostratigraphy of the Bull Canyon Formation (Chinle Group, Upper Triassic), east-central New Mexico with revisions of the families Metoposauridae (Amphibia: Temnospondyli) and Parasuchidae (Reptilia: Archosauria) [Ph.D. dissertation]: Albuquerque, University of New Mexico, 404 p.
- Hunt, A. P., 2001, The vertebrate fauna, biostratigraphy and biochronology of the type Revueltian faunachron, Bull Canyon Formation (Upper Triassic), east-central New Mexico: New Mexico Geological Society Guidebook, v. 52, p. 123-152.
- Hunt, A. P., and Lucas, S. G., 1993, Stratigraphy and vertebrate paleontology of the Chinle Group (Upper Triassic), Chama Basin, north-central New Mexico: New Mexico Museum of Natural History and Science Bulletin, v. 2, p. 61-69.
- Hunt, A. P., Lucas, S. G., Heckert, A. B., Sullivan, R. M., and Lockley, M. G., 1998, Late Triassic dinosaurs from the western United States: Geobios, v. 31, p. 511-531.
- Ivie, M. A., Slipinski, S. A., and Wegrzynowicz, P., 2001, Generic homonyms in the Colydiinae (Coleoptera: Zopheridae): Insecta Mundi, v. 15, no. 1, p. 63-64.
- Long, R. A., and Murry, P. A., 1995, Late Triassic (Carnian and Norian) tetrapods from the southwestern United States: New Mexico Museum of Natural History and Science Bulletin, v. 4, p. 254 p.
- Lucas, S. G., 1993, The Chinle Group: Revised stratigraphy and biochronology of Upper Triassic strata in the western United States: Museum of Northern Arizona, Bulletin, v. 59, p. 27-50.
- Lucas, S. G., 1997, The Upper Triassic Chinle Group, western United States, non-marine standard for Late Triassic time, in Dickins, J. M., Yang, Z., Yin, H., Lucas, S. G., and Acharyya, S. K., eds., Permo-Triassic of the Circum-Pacific: Cambridge, Cambridge University Press, p. 200-228.
- Lucas, S. G., 1998, Global Triassic tetrapod biostratigraphy and biochronology: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 143, p. 347-384.
- Lucas, S. G., and Hunt, A. P., 1992, Triassic stratigraphy and paleontology, Chama

- basin and adjacent areas, north-central New Mexico: New Mexico Geological Society, Guidebook, v. 43, p. 151-167.
- Lucas, S. G., and Hunt, A. P., 1993, Tetrapod biochronology of the Chinle Group (Upper Triassic), western United States: New Mexico Museum of Natural History and Science Bulletin, v. 3, p. 327-329.
- Lucas, S. G., Hunt, A. P., and Long, R. A., 1992, The oldest dinosaurs: *Naturwissenschaften*, v. 79, p. 171-172.
- Lucas, S. G., Anderson, O. J., and Hunt, A. P., 1994, Triassic stratigraphy and correlations, southern High Plains of New Mexico-Texas: New Mexico Bureau of Mines & Mineral Resources Circular 150, p. 105-126.
- Lucas, S. G., Heckert, A. B., and Hunt, A. P., 2001, Triassic stratigraphy, biostratigraphy and correlation in east-central New Mexico: New Mexico Geological Society, Guidebook 53, p. 85-102.
- Norman, D. B., 1990, Problematic Theropoda: "Coelurosaurs", in Weishampel, D. B., Dodson, P., and Osmólska, H., eds., *The Dinosauria*: Berkeley, University of California Press, p. 280-305.
- Ostrom, J. H., 1981, *Procompsognathus*—Theropod or thecodont?: *Palaeontographica Abteilung A*, v. 175, p. 179-195.
- Padian, K., 1986, On the type material of *Coelophysis* Cope (Saurischia: Theropoda) and a new specimen from the Petrified Forest of Arizona (Late Triassic: Chinle Formation), in Padian, K., ed., *The beginning of the age of dinosaurs: Faunal change across the Triassic-Jurassic boundary*: Cambridge, Cambridge University Press, p. 45-60.
- Raath, M., 1977, The anatomy of the Triassic theropod *Syntarsus rhodesiensis* (Saurischia: Podokesauridae) and a consideration of its biology [Ph.D. thesis]: Rhodes University, 353 p.
- Raath, M. A., 1990, Morphological variation in small theropods and its meaning in systematics: evidence from *Syntarsus rhodesiensis*, in Carpenter, K., and Currie, P. J., eds., *Dinosaur systematics: Approaches and perspectives*: Cambridge, Cambridge University Press, p. 91-106.
- Rowe, T., and Gauthier, J., 1990, Ceratosauria, in Weishampel, D. B., Dodson, P., and Osmólska, H., eds., *The Dinosauria*: Berkeley, University of California Press, p. 151-168.
- Sereno, P. C., and Wild, R., 1992, *Procompsognathus*: theropod, "thecodont" or both?: *Journal of Vertebrate Paleontology*, v. 12, p. 435-458.
- Small, B. J., 1989, Post quarry, in Lucas, S. G., and Hunt, A. P., eds., *Dawn of the Age of Dinosaurs in the American Southwest*: Albuquerque, New Mexico Museum of Natural History, p. 145-148.
- Sullivan, R. M., and Lucas, S. G., 1999, *Eucoelophysis baldwini*, a new theropod dinosaur from the Upper Triassic of New Mexico, and the status of the original types of *Coelophysis*: *Journal of Vertebrate Paleontology*, v. 19, p. 81-90.
- Sullivan, R. M., Lucas, S. G., Heckert, A. B., and Hunt, A. P., 1996, The type locality of *Coelophysis*, a Late Triassic dinosaur from north-central New Mexico (U.S.A.): *Paläontologische Zeitschrift*, v. 70, p. 245-255.
- Tykoski, R. S., 1998, The osteology of *Syntarsus kayentakatae* and its implications for ceratosaurid phylogeny [M.S. thesis]: Austin, University of Texas, 217 p.
- Zeigler, K. E., 2002, A taphonomic analysis of a fire-related Upper Triassic fossil assemblage [M.S. thesis]: Albuquerque, University of New Mexico, 124 p.
- Zeigler, K. E., 2003, Taphonomic analysis of the Snyder quarry: A fire-related Upper Triassic vertebrate fossil assemblage from north-central New Mexico: New Mexico Museum of Natural History and Science, Bulletin 24, p. 49-62.
- Zeigler, K. E., Lucas, S. G., and Heckert, A. B., 2002, A phytosaur skull from the Upper Triassic Snyder quarry (Petrified Forest Formation: Chinle Group) of north-central New Mexico: New Mexico Museum of Natural History and Science Bulletin, v. 21, p. 171-177.

